Development of feeding and swimming functions in larvae of *Chionodraco rastrospinosus* (Channichthyidae)

by

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ABSTRACT. - The development of characters related to feeding and swimming in *Chionodraco rastrospinosus* Dewitt & Hureau, 1979 larvae was examined in 35 specimens (24.5-45.4 mm standard length, SL) collected from the Indian Ocean sector of the Southern Ocean. Of these, 16 larvae were cleared and stained to examine osteological development. Larvae of 26 mm SL appeared capable of grasping, biting, and sucking feeding based on their possession of fundamental oral cavity elements and teeth. Furthermore, feeding function improved with element growth and tooth increase until 35-37 mm SL. The complete pectoral fin ray number was attained at ca. 35 mm SL. The pelvic and pectoral fin lengths increased rapidly by ca. 37 mm SL. Vertebrae were first observed at 38.3 mm SL, but neither dorsal nor anal fin elements appeared until 40.3 mm SL. The delayed formation of the vertebrae and dorsal and anal fins indicates that the larvae do not swim actively using caudal propulsion. Swimming is accomplished by paired-fin development until 35-37 mm SL, and is enhanced by the development of vertebrae and caudal fin elements thereafter. *Chionodraco rastrospinosus* larvae until 35-37 mm SL are inferred to be ambush-style predators with early development of feeding function, in contrast to their slowly developed swimming function.

RÉSUMÉ. - Développement des fonctions alimentaires et de nage des larves de *Chionodraco rastrospinosus* (Channichthyidae).

Le développement des caractères associés à la nutrition et à la nage des larves de *Chionodraco rastrospinosus* Dewitt & Hureau, 1979 a été examiné sur 35 spécimens (24,5-45,4 mm LS) capturés dans le secteur indien de l'Océan Austral. Seize de ces larves ont été éclaircies et colorées pour étudier le développement ostéologique. Les larves de 26 mm (LS) sont capables d'attraper, mordre et gober en raison de la présence d'éléments essentiels de la cavité orale et de leurs dents. Les fonctions nutritives s'améliorent avec la croissance de ces éléments et des dents jusqu'à une taille de 35 à 37 mm. Le nombre total de rayons des nageoires pectorales est atteint à une taille de 35 mm. Les longueurs des nageoires pelviennes et pectorales augmentent rapidement à partir de 37 mm. Les vertèbres sont observées à partir de 38,3 mm, mais les nageoires dorsale et anale n'apparaissent qu'à partir de 40,3 mm. Le retard dans la formation des vertèbres et des nageoires dorsales et anales indique que les larves ne nagent pas activement par propulsion caudale. La nage s'effectue grâce aux nageoires paires jusqu'à 35-37 mm et est aidée par le développement des vertèbres et de la nageoire caudale après 35-37 mm. Les larves de *Chionodraco rastrospinosus* peuvent être considérées comme des prédateurs par embuscade avec un développement précoce des fonctions de nutrition, en contraste avec le développement lent des fonctions de nage.

Key words. - Channichthyidae - *Chionodraco rastrospinosus* - PSE - Southern Ocean - Icefish - Larvae - Osteological development.

The biology of notothenioid fishes, most of which are limited to the Southern Ocean, has been well studied, including their systematics, physiology, and reproduction, especially as it pertains to adaptation to extremely cold waters or fishery resources (Kock, 1992; Eastman, 1993). As for larval notothenioids, there is fragmentary knowledge of the taxonomy and early life history for several species (e.g., Loeb *et al*., 1993; Koubbi *et al*., 1990; North, 2001). The early pelagic life lasts for at least one year, until individuals attain a relatively large size (Kellermann, 1989; Loeb *et al*., 1993). For example, in the notothenioid family Channichthyidae, larvae and juveniles exceeding 40 mm in standard length (SL) are commonly pelagic (Kellermann, 1986, 1989). However, little is known of how such large larvae adapt to a pelagic life in terms of functional morphology.

The development of feeding and swimming functions can be inferred from the morphological development of several characters, such as the jaws and the bones forming the oral cavity, fins, and the axial skeleton (Kohno, 1998; Moteki *et al*., 2002). Knowledge of functional development is useful for understanding larval ecology (Taki *et al*., 1987; Funahashi *et al*., 2003). Osteological developments of notothenioid fishes are well studied by a series of Voskoboinikova's works (e.g., Voskoboinikova, 1997; Voskoboinikova and Bruce, 2001). However, these studies do not aim to examine functional development, but to discuss mainly phylogenetic relationships within the Notothenioidei.

Therefore, this study examined osteological development in a view point of functional morphology in order to clarify the development of swimming and feeding related charac-

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ters in larvae of the channichthyid fish, *Chionodraco rastrospinosus* Dewitt and Hureau, 1979, collected from the eastern part of the Indian Ocean sector of the Southern Ocean.

MATERIALS AND METHODS

Thirty-five larvae (24.5 to 45.4 mm SL, Tab. I) were collected from the Indian Ocean sector of the Southern Ocean using a rectangular mid-water trawl (RMT 1+8) (Baker *et al.*, 1973) and a ring net (mouth diameter: 1.3 m, mesh size: 0.33 mm) during the cruise of TR/V *Umitaka-maru*, Tokyo University of Marine Science and Technology (TUMSAT), on 4 February 2003. Larvae were fixed by 5% buffered formalin immediately on board and preserved in 70% ethanol in laboratory.

For all of the larvae, standard length (SL), head length, upper jaw length, and pectoral and pelvic fin lengths were measured under a binocular microscope with a micrometer or using a calliper. Sixteen of these specimens (25.5-40.3 mm SL; Tab. I) were cleared and stained following Potthoff (1984) to examine the developmental states of the cartilage and bones, and to count the numbers of jaw and pharyngeal teeth (on the left side). Larval lengths in the following descriptions refer to the SL.

Identification

Specimens were identified as *Chionodraco rastrospinosus* according to Kellermann's (1989) description based on larvae (20-60 mm) collected around the Antarctic Peninsula. Our specimens were very similar to his descriptions with respect to the following characters: two to six melanophores along each myoseptum, forming several longitudinal rows on the lateral side of the body; melanophores scattered on the anterior part of the dorsal and anal finfold in small larvae (24.5-30.0 mm), which extend posteriorly with development (34.3-45.4 mm); pelvic fin having dense melanophores on the fin membrane between the spine and first ray and along the other rays; pelvic fin not reaching far beyond the anus; rostral spine present.

Table I. - List of *Chionodraco rastrospinosus* larvae examined in this study. SL: standard length (mm). *: Cleared and stained specimens. A: 66°27.76'S, 139°52.88'E; B: 65°54.72'S, 139°55.86'E; C: 66°27.76'S, 139°52.88'E; D: 65°48.85'S, 139°55.41'E; E: 65°37.91'S, 139°53.33'E *[Liste des larves de* C. rastrospinosus *examinées dans ce travail.]*

MTUF-P (L)	SL	Locality	Gear
21937	24.5	B	RMT
21909*	25.5	A	RMT
21920*	25.6	A	RMT
21925	25.9	A	RMT
21907	26.2	A	RMT
21914	26.8	A	RMT
21912*	26.8	A	RMT
21913*	26.9	A	RMT
21910	27.8	A	RMT
21911*	27.9	A	RMT
21908	28.3	A	RMT
uncat.	29.9	A	RMT
21916	30.0	A	RMT
21935	34.3	B	RMT
21915*	34.5	A	RMT
21922*	34.7	A	RMT
21928*	35.4	A	RMT
21917*	35.8	A	RMT
21936	35.9	B	RMT
uncat.	36.2	C	RMT
21921	36.3	A	RMT
21931	36.8	A	RMT
21929*	36.8	A	RMT
21923*	37.1	A	RMT
21924	37.5	A	RMT
21919*	38.3	A	RMT
21930	38.5	A	RMT
21932*	38.5	A	RMT
21927	38.6	A	RMT
21926*	39.5	A	RMT
21938	39.6	D	Ring net
21918*	40.3	A	RMT
21933	40.3	B	RMT
21939	40.5	E	Ring net
21934	45.4	B	RMT

RESULTS AND DISCUSSION

A note on identification

The genus *Chionodraco* includes three species: *C. rastrospinosus*, *C. hamatus*, and *C. myersi* (Gon and Heemstra, 1990). Larval or juvenile stages were described by Kellermann (1989) for *C. rastrospinosus* and by Efremenko (1979) for *C. hamatus*. Gon (1988) described pelagic postlarvae of *C. hamatus* and *C. myersi*. The larvae examined in this study do not match Gon's (1988) description for *C. hamatus* (*i.e.*, having no rostral spine and "pale" pelvic fin), as our specimen had a rostral spine and a partly pigmented pelvic fin. Furthermore, our specimens differed from *C. myersi*, as described by Gon (1988), in which *C. myersi* has black pelvic fin membrane. The description of *C. hamatus* by Efremenko (1979) almost agrees with the features of Kellermann's (1989) *C. rastrospinosus* and those of our specimens. Efremenko (1979) described specimens taken off the South

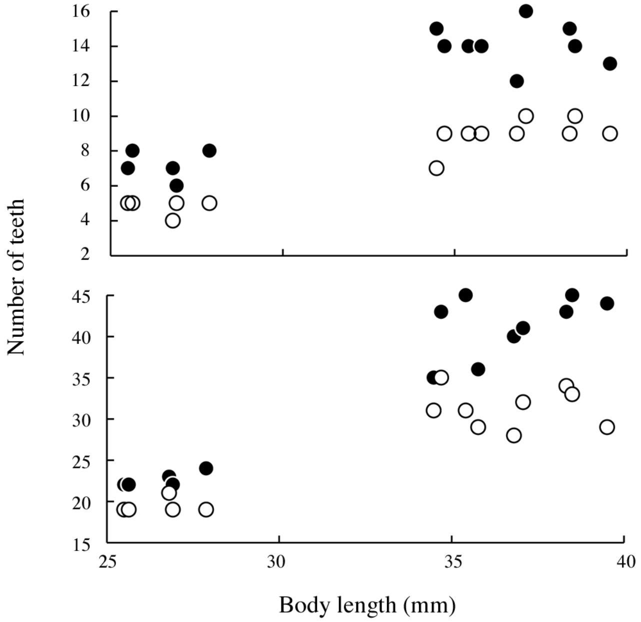

Figure 1. - Development of pharyngeal (top) and oral teeth (bottom) in the larval icefish *Chionodraco rastrospinosus*. ●: upper teeth; ○: lower teeth. *[Développement des dents des mâchoires (haut) et des dents pharyngiennes (bas) chez les larves de poisson des glaces* C. rastrospinosus. ● *: dents supérieures ;* ○ *: dents inférieures.]*

Orkney Islands, in the Scotia Sea, near the Antarctic Peninsula. However, adult *C. hamatus* have never been recorded in those waters, while records of adult *C. rastrospinosus* are limited to the Antarctic Peninsula. Therefore, the *C. hamatus* of Efremenko (1979) is likely to be *C. rastrospinosus*. Although there are no records of *C. rastrospinosus* from the Indian Ocean sector, we tentatively identified our specimens as *C. rastrospinosus*.

Feeding function

The 25.5-mm cleared and stained larva possessed the fundamental components of the oral cavity (Tab. II): bony elements of upper and lower jaws, parasphenoid roof, cartilaginous lower branchial arch and hyoid arch forming the cavity floor, and the suspensorium making up the side. Both pharyngeal (5 and 7-8 in upper and lower, respectively) and jaw teeth (22 and 19) were present in 25.5 and 25.6 mm (Fig. 1). These results suggest that the larvae acquire grasping and biting functions by 26 mm, in addition to suction feeding by negative pressure produced in the expanded oral cavity (Otten, 1982; Kohno, 1998).

The enhanced feeding ability supported by the growth of elements (head and upper jaw length, Fig. 2A) until ca. 37 mm and the increase of teeth continues until ca. 35 mm (Fig. 1). Thereafter, growth of relative head length slowed and teeth number levelled off. Some bone elements of the neurocranium (ectoethmoid bar, sphenotic and prootic) first appear at 35-40 mm (Tab. II), and they enhance the rigidity of the neurocranium, supporting the steady movement of some elements articulated with the neurocranium, such as the suspensorium (palato-quadrate cartilage, ectopterygoid and hyomandibular-symplectic cartilage) and branchial arch (ceratobranchial-1 to -4) that first appear of ossifying at around 35 mm (Tab. II). Consequently, *Chionodraco rastrospinosus* larvae develop feeding function in terms of element

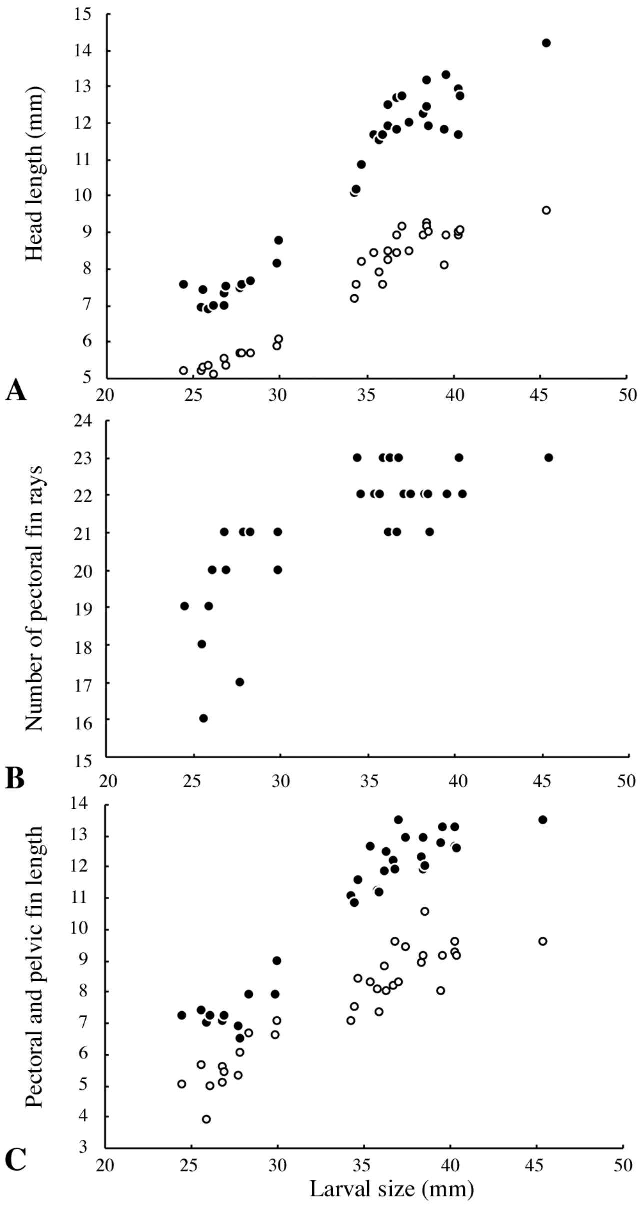

Figure 2. - Larval icefish *Chionodraco rastrospinosus*. **A**: Development in head length (●) and upper jaw-length (○); **B**: Number of pectoral fin-rays; **C**: Pectoral (●) and pelvic (○) fin-length. *[Larves de poisson des glaces* C. rastrospinosus. ***A** : Développement de la longueur de la tête* (●) *et de la mâchoire inférieure* (○) *;* ***B** : Nombre de rayons pectoraux ;* ***C** : Longueur des nageoires pelviennes* (○) *et pectorales* (●)*.]*

Table II. - Standard length (in mm) in which osteological events first occurred in *Chionodraco rastrospinosus* larvae. *: New bone appearance or ossification of cartilaginous element. *[Longueurs standard auxquelles apparaissent les éléments osseux chez les larves de* C. rastrospinosus.*]*

Cartilage and bone element	Cartilage	Bone*
Upper jaw		
Maxilla		25.5
Premaxilla		25.5
Teeth		25.5
Lower jaw		
Meckel's cart.	25.5	
Dentary		25.5
Angular		25.5
Retroarticular		25.5
Teeth		25.5
Suspensorium		
Palatine	34.7	
Palato-quadrate cart.	25.5	34.5
Ectopterygoid		35.8
Hyomandibular-symplectic cart.	25.5	35.8
Hyoid arch		
Hypohyal	25.5	
Ceratohyal-epihyal cart.	25.5	
Interhyal	25.5	40.5
Branchiostegal ray		25.5
Basihyal	25.5	
Lower branchial arch		
Basibr.	25.5	
Hypobr. -1	25.5	
-2	25.5	
-3	25.5	
Isolated cart. basibr.	39.5	
Ceratobr. -1	25.5	34.5
-2	25.5	35.8
-3	25.5	35.8
-4	25.5	35.8
-5	27.9	
Upper branchial arch		
Epibr. -1	34.5	
-2	34.5	
-3	34.5	
-4	34.5	
Pharyngobr. -2	25.5	
-3	25.5	
Opercular bones		
Opercle		25.5
Preopercle		25.5
Subopercle		25.5
Interopercle		26.8
Neurocranium		
Auditory capsule	25.5	
Frontal		25.5
Ectethmoid bar	36.8	
Sphenotic		40.3
Prootic		34.5
Parasphenoid		25.5
Nasal		38.5
Suborbital bones		
Lachrymal		25.5
Fin supports and vertebrae		
Cleithrum		25.5
Coraco-scapular cart.	25.5	
Supracleithrum		25.5
Posttemporal		26.8
Basipterygium		34.5
Hypural	25.5	35.8
Urostyle		34.5

growth and teeth formation by 35-37 mm, and thereafter the feeding function is enhanced by the ossification of cartilaginous elements and the appearance of new bone elements.

Voskoboinikova (1997) mentioned that, in some channichthyid species, the role of hyoid and gill arches, angular and opercular bones to create negative pressure for respiration and suction feeding probably had reduced due to cutaneous respiration being important in channichthyids rather than gill respiration, although there is controversy as to how cutaneous respiration is important for notothenioids (Eastman, 1993). However, well developed jaw would indicate that sucking function for feeding is less important than grasping and biting function even in the early stage of channichthyid larvae.

Swimming function

A 25.5-mm larva possessed the full number of principal caudal-fin rays (5 + 6), with the notochord flexion nearly completed (completed by 26.8 mm). There were 16-19 pectoral-fin rays in the 24.5-25.9-mm larva (Fig. 2B). Pectoral girdle elements (cleithrum, coraco-scapular cartilage, supracleithrum and posttemporal) were observed by 25.5 mm (Tab. II). All pelvic-fin rays were present (I, 5) in the 24.5-mm larva.

Enhancement of swimming function through 35-37 mm is supported by paired-fin development. Pectoral fin ray number and both pectoral and pelvic fin lengths growth levelled off thereafter (Fig. 2B, C). Paired fins stabilize the body and support manoeuvrability rather than forward propulsion (Gosline, 1971). As for the dorsal and anal fins, neither fin supports nor fin rays appeared until 40.3 mm. Larvae start ossification of the hypurals and urostyle at 35-36 mm (Tab. II). Fourteen vertebral centra were first observed in 38.3 mm, and three to 20 between 38.5-40.3-mm larvae (59-62 in adult complement, Gon and Heemstra, 1990). Furthermore, neural and hemal spines are absent in the size range examined. Therefore, after 35-36 mm, the larvae enhance swimming ability by increasing axial skeleton and caudal elements. Caudal propulsion, which most adult teleosts undertake, requires a developed muscular system attached to the axial skeleton (Gosline, 1971). Larvae having neither vertebrae nor dorsal and anal fins undertake beat and glide swimming (Hunter, 1981), rather than active forward propulsion using caudal locomotion (Gosline, 1971).

Estimated behaviour

This study showed that *Chionodraco rastrospinosus* larvae delay ossification, especially for swimming-related characters. Delayed ossification in *Chionodraco rastrospinosus*, which lack a gas bladder, would reduce the specific gravity, and allow larvae to remain in the water column (Eastman, 1993). It is functionally disadvantageous to reduce the ossification of swimming-related characters, which are needed to chase food organisms. However, *Chionodraco rastrospinosus* larvae could lie in wait for food organisms in the water column with the earlier developed feeding function.

In 35-37 mm, a lot of developmental events, such as ossification, levelled-off growth and new appearance of bone elements, take place, indicating that larvae would change their behaviour. Larvae longer than around 35 mm with increased specific gravity may attain neutral buoyancy in deeper, higher-density waters, and change feeding habits, prior to settlement.

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REFERENCES

BAKER A. de, CLARKE M.R. & M.J. HARRIS, 1973. - The N.I.O. combination net (RMT 1+8) and further developments of Rectangular Midwater Trawls. *J. Mar. Biol. Ass. UK*, 53: 167-184.

EASTMAN J.T., 1993. - Antarctic Fish Biology. Evolution in a Unique Environment. 322 p. San Diego: Academic Press.

EFREMENKO V.N., 1979. - Description of the larvae of six species of the family Channichthyidae from Scotia Sea. *J. Ichthyol.*, 19: 65-75.

FUNAHASHI N., SUZUKI M., UCHIDA N., KOHNO H., MOTEKI M., MURAI N., IMAI H. & M. KUBOTA, 2003. - Diet and functional morphology of largemouth bass, *Micropterus salmoides*, larvae, juvenile and young at Hibiya Imperial Moat in central Tokyo. *J. Tokyo Univ. Fish.*, 90: 1-11. [In Japanese with English abstract]

GON O., 1988. - The fishes collected during the South African SIBEX I + II expeditions to the Indian Ocean sector of the Southern Ocean (60-66ºS, 48-64ºE). *South Afr. J. Antarct. Res.*, 18: 55-70.

GON O. & P.C. HEEMSTRA (eds), 1990. - Fishes of the Southern Ocean. 462 p. Grahamstown: J.L.B. Smith Institute of Ichthyology.

GOSLINE W.A., 1971. - Functional Morphology and Classification of Teleostean Fishes. 208 p. Honolulu: The Univ. Press of Hawaii.

HUNTER J.R., 1981. - Feeding ecology and predation of marine fish larvae. *In*: Marine Fish Larvae (Lasker R., ed.), pp. 33-77. Washington: Washington Sea Grant Program.

KELLERMANN A., 1986. - On the biology of early life stages of notothenioid fishes (Pisces) off the Antarctic Peninsula. *Ber. Polarforsch.*, 31: 1-148.

KELLERMANN A., 1989. - Catalogue of early life stages of Antarctic notothenioid fishes. *BIOMASS Sci. Ser.*, 10: 45-136.

KOCK K.-H., 1992. - Antarctic Fish and Fisheries. 376 p. Cambridge: Cambridge Univ. Press.

KOHNO H., 1998. - Early life history features influencing larval survival of cultivated tropical finfish. *In*: Tropical Mariculture (De Silva S.S., ed.), pp. 71-111. London: Academic Press.

KOUBBI P., DUHAMEL G. & P. CAMUS, 1990. - Early life stages of Notothenioidei from the Kerguelen Islands. *Cybium*, 14(3): 225-250.

LOEB V.J., KELLERMANN A.K., KOUBBI P., NORTH A.W. & M.G. WHITE, 1993. - Antarctic larval assemblages: A review. *Bull. Mar. Sci.*, 53: 416-449.

MOTEKI M., ISHIKAWA T. & H. FUSHIMI, 2002. - Changes in feeding function inferred from osteological development in the early stage larvae of the Japanese flounder, *Paralichthys olivaceus*, reared in the laboratory. *Suisanzoshoku*, 50: 285-294.

NORTH A.W., 2001. - Early life history strategies of notothenioids at South Georgia. *J. Fish Biol.*, 58: 496-505.

OTTEN E., 1982. - The development of a mouth-opening mechanism in a generalized *Haplochromis* species: *H. elegans* Trewavas, 1933 (Pisces, Chiclidae). *Neth. J. Zool.*, 32: 31-48.

POTTHOFF T., 1984. - Clearing and staining techniques. *In*: Ontogeny and Systematics of Fishes (Moser H.G., Richards W.J., Cohen D.M., Fahay M.P., Kendall Jr. & S.L. Richardson, eds), pp. 35-37. American Society of Ichthyology Herpetology, Spec. Publ. 1.

TAKI Y., KOHNO H. & S. HARA, 1987. - Morphological aspects of the development of swimming and feeding functions in the milkfish *Chanos chanos*. *Jpn. J. Ichthyol.*, 34: 198-208.

VOSKOBOINIKOVA O.S., 1997. - Osteological development of the Channichthyidae (Teleostei: Notothenioidei). *Cybium*, 21(4): 369-379.

VOSKOBOINIKOVA O.S. & B. BRUCE, 2001. - Development of bony skeleton during ontogeny of *Bovichtus anguistifrons* (Bovichthydae, Notothenioidei) with comparative notes on development of bony skeleton of congolli *Pseudahritis urvilli* (Pseudaphritidae). *J. Ichthyol.*, 41: 57-66.

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